

FIRE MAINTENANCE AND ARTIFICIAL BURROWS INCREASE GROWTH AND
SURVIVAL OF THE ENDANGERED DUSKY GOPHER FROG IN LONGLEAF PINE
FORESTS

A thesis presented to the faculty of the Graduate School of
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By

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"I know the human being and fish can coexist peacefully." - George W. Bush Jr.

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ABSTRACT

FIRE MAINTENANCE AND ARTIFICIAL BURROWS INCREASE GROWTH AND SURVIVAL OF THE ENDANGERED DUSKY GOPHER FROG IN LONGLEAF PINE FORESTS

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The critically endangered Dusky Gopher Frog occupies longleaf pine savannas frequented by fire, where grasses and natural burrows are abundant. Gopher frogs avoid fire-suppressed habitat, where the understory is comprised of shrubs and there are fewer burrows. It is assumed that fire-suppression creates a suboptimal environment for gopher frogs, but there are few data to support this. In this experiment, I examined growth and survival rates of juvenile dusky gopher frogs in burned and fire-suppressed habitats and, using artificial burrows, I examined how burrow density affected these rates. I marked and released newly metamorphosed frogs into outdoor enclosures in a longleaf pine forest assigned to one of four treatments: frequently-burned, frequently-burned with artificial burrows, fire-suppressed, and fire-suppressed with artificial burrows. From June 2018 through January 2019, I recaptured frogs and recorded their mass and snout-vent length. I found that frogs in frequently-burned enclosures containing artificial burrows had the greatest growth. Frogs in fire-suppressed enclosures without artificial burrows had the lowest growth. Frogs in the frequently-burned enclosures without artificial burrows and frogs in fire-suppressed enclosures with artificial burrows had strikingly similar growth, demonstrating that increasing burrow density could mitigate the effects of fire-suppression. Survival was highest in frequently-burned enclosures containing artificial burrows. The results of this research suggest that both

controlled burns and artificial burrows can increase growth in gopher frogs while the combination of the two treatments can enhance survival. Management burns and incorporating artificial burrows into forest management strategies could facilitate the recovery of this endangered species.

INTRODUCTION

Amphibians play important roles in their ecosystems. They can reach a high biomass (Burton & Likens, 1975) and function in the cycling of nutrients from aquatic and terrestrial communities as both predator and prey in food webs (Seale, 1980; Semlitsch, 2003). Amphibians are also some of the most threatened animals in the world (Stuart et al., 2004). Many of the threats facing amphibians come from environmental changes, habitat loss and degradation, disease, contaminants, and other anthropogenic impacts (Stuart et al., 2004). Human activity continues to diminish the quality of these organisms' habitats, which has led to reductions in range sizes and habitat connectivity. This can further imperil these animals by reducing their genetic diversity (Richter et al., 2009). Global population declines in amphibians are putting many species at risk of extinction. Conservation efforts and recovery of these organisms should be a high priority.

The dusky gopher frog, *Rana sevosa*, is one of the most endangered amphibian species in the world. It was listed as critically endangered in 2001 by the U. S. Fish and Wildlife Service and has since been closely monitored by various research and conservation groups (United States Fish and Wildlife Service [USFWS], 2001; USFWS, 2015). Habitat loss and alteration have severely impacted these frogs' population numbers. Their range once spanned the southeastern United States along the Gulf Coast from southwestern Alabama to southeastern Louisiana (Goin & Netting, 1940; Young & Crother, 2001), but it is now confined to 3 counties in southern Mississippi. Recovery efforts include monitoring the dusky gopher frogs' population, designating critical habitat, restoring dusky gopher frog habitats, and translocating frogs to

restored areas (USFWS, 2012; USFWS, 2015). Areas that have dusky gopher frog populations are now federally protected from new development and other inimical activities (USFWS, 2001).

The dusky gopher frog requires ephemeral, open canopy ponds for breeding and larval development (Thurgate & Pechmann, 2007). Ephemeral ponds go through cycles of flooding after heavy rains and then dry temporarily, creating habitats that are free of predatory fishes. After metamorphosis the dusky gopher frog occupies burrows in longleaf pine uplands that were naturally on a two to three-year burn cycle (Richter et al., 2001; Tupy, 2012). Connectivity of both terrestrial and aquatic habitats is necessary for the completion of these frogs' life cycle. Most of their adult lives are spent within their burrows and they usually venture out only for breeding or for foraging on their pads (Goin & Netting, 1940). A burrowing frog's pad is a patch of soil located just outside of the entrance of a burrow. *Rana sevosa* uses its pad as a basking and feeding location. Frogs will sit and ambush food items, primarily arthropods and other invertebrates (Goin & Netting, 1940), that come in the vicinity of their pads. Since the pad is just outside of the burrow, the frog can easily return to the protection of the burrow if it senses any danger.

Dusky gopher frogs do not create burrows for themselves. The name "gopher frog" comes from their affinity for taking up residency in burrows constructed by the gopher tortoise, *Gopherus polyphemus*. Gopher tortoise burrows have been found to house over 350 other species (Jackson & Milstrey, 1989; Pike & Mitchell, 2013). The observation of gopher tortoises was once a good indicator of the presence of *R. sevosa*. However, these frogs can also be found in burrows made by small mammals such as field mice, as well as stump holes and root tunnel systems carved out by fire or natural decay (Richter et al., 2001).

Fire-suppressed longleaf pine forests offer fewer available burrows for the dusky gopher frog than frequently-burned habitat (Tupy, 2012). Fire maintenance in longleaf pine forests promotes herbaceous vegetation growth that attracts gopher tortoises and small mammals that make burrows (Means, 2005). The increase in herbaceous growth offers these animals greater foraging opportunities and refuge from predatory animals. Longleaf pine forests' exposure to periodic fire thus has a cascade of benefits for the dusky gopher frog.

Gopher frogs select frequently-burned over fire-suppressed terrestrial habitat (Tupy, 2012; Roznik & Johnson, 2009a; Roznik & Johnson, 2009b). Gopher frogs likely experience critical fitness-related consequences associated with habitat selection behavior, including higher growth and survivorship. I hypothesized that overall survival and growth of the gopher frog would be greater in frequently-burned habitat than in fire-suppressed habitat, in part because of the greater availability of burrows (Roznik & Johnson, 2009a). If so, could the presence of artificial burrows improve growth and survival in either fire-maintained or fire-suppressed habitat? I hypothesized that artificial burrows would increase the gopher frogs' growth and survival, especially in the fire-suppressed habitat, where burrows are more scarce. I also hypothesized that artificial burrows would be used more in the fire-suppressed habitat, where natural burrows are more limited than in fire-maintained habitat.

It is possible that *R. sevosia* select frequently-burned over fire suppressed habitat based on the thermal characteristics of these sites. Perhaps the structural alterations of microhabitats created by fire improve physiological performance in these ectothermic animals by allowing more solar radiation through to the forest floor than in fire-suppressed forests (Huey, 1991). I examined temperatures in various microhabitats within frequently-burned and fire-suppressed habitats, as well as vegetation characteristics, to understand how microclimates could influence

habitat selection in these animals (Huey, 1991). I hypothesized that the open canopies of fire-maintained sites may result in greater variation in ground surface temperature, but that the burrows would provide a refuge when temperatures got too high (Pike & Mitchell, 2013; Heemeyer et al., 2012). Such spatial variation in temperatures could facilitate behavioral thermoregulation and improve growth and survival.

Another possibility is that *R. sevosa* habitat selection is based on the availability of food resources. In areas with abundant prey availability, *R. sevosa* would have little need to venture far away from the protection of its burrow. The frog could sit in its burrow or on its pad at the entrance of the burrow and have arthropods and other invertebrates come to it. In habitat with little available food, frogs would need to leave their burrows and spend time hunting for prey. This would require energy expenditure, and expose frogs to greater risk of predation, evaporative water loss, and overheating (Blihovde, 2006; Roznik & Johnson, 2009a). I investigated the availability of arthropod food sources in unburned and recently burned habitats. I hypothesized that the availability of prey would be greater in areas that are managed by fire than in fire-suppressed habitats. The growth of new herbaceous vegetation after fires could be attractive to insects (New, 2014). This would in turn create greater foraging opportunities for *R. sevosa* both inside and near the entrance of their burrows.

METHODS

Gopher frogs were raised from eggs collected from Glen's Pond in Harrison County, Mississippi during February 2018. Approximately 30 percent of each of 44 gopher frog egg masses was reared in the laboratory until hatching. Once the tadpoles absorbed their yolk sacs and became free-swimming, 20 were placed in each of 57, 1325-liter cattle tanks (1.8 m diameter, 0.6 m height) and raised until they metamorphosed into juveniles. This experiment used 480 of the metamorphosed frogs produced from 40 of the 57 tanks. Cattle tanks were filled with approximately 1000 L of well water. One kilogram of dried *Juncus repens*, a local rush, was placed in each tank to imitate natural litter found in local open-canopy ponds. Algae and zooplankton from Glen's Pond were collected and used to inoculate the tanks prior to introducing tadpoles, and tanks were supplemented with additional algae and zooplankton monthly thereafter to help establish a realistic pond community (Wilbur, 1987). A mesh net was placed over the top of each tank to prevent any foreign items, including dragonfly larvae (Odonata) or other frogs, from entering. The tadpoles were fed six algae wafers per tank each week, which has been shown to promote growth similar to that of tadpoles found in natural ponds (Smith et al., 2018).

After metamorphosis, juvenile frogs were moved to terrestrial enclosures. Each enclosure was 15 x 15 m (225 m²; Fig. 1), with walls made of a thin sheet of solid aluminum flashing which extended approximately 0.6 m aboveground, and 0.3 m underground. This was adequate to ensure that the frogs could not leave the enclosures and that no other gopher frogs entered. Four pairs of enclosures (8 enclosures total) were located in an area where fire is regularly prescribed, and four pairs (8 enclosures total) were located in an adjacent fire-suppressed site.

Enclosures were constructed in 2005 for a previous experiment, and their respective fire treatments have been generally maintained inside and outside the enclosures since their construction, with a fire-return interval of approximately every 3 years. The enclosures were located 456 to 1033 m away from the center of Glen's Pond. The habitat in the frequently-burned sites consisted of longleaf pine forest uplands with an understory dominated by forbs and grasses such as little bluestem (*Schizachyrium scoparium*). The area in and around these enclosures was burned on 12 April 2018 (39-48 days before frogs were released in the enclosures). The habitat in the fire-suppressed area consisted of longleaf pine forest uplands with a dense understory dominated by the shrub yaupon holly (*Ilex vomitoria*). The habitat inside these enclosures had not been regularly maintained by fire. Each pair of fire-maintained habitat enclosures was adjacent to a pair of fire-suppressed habitat enclosures, with the two being separated by 99 – 210 m and a United States Forest Service road. Each pair of fire-maintained enclosures and their adjacent fire-suppressed enclosures was defined as a spatial block. The distance between the northernmost and southernmost enclosure was 1134 m in the fire-maintained habitat and 1533 m in the fire-suppressed habitat. The distance between blocks was 161 – 590 m in fire-maintained habitat and 169 – 871 m in fire suppressed habitat.



Figure 1. A pair of fire-maintained enclosures (left) and fire-suppressed enclosure (right)

Thirty artificial burrows were evenly placed in one of each pair of enclosures randomly selected. The remaining enclosure in each pair served as a control. Artificial burrows were laid out in a grid with each burrow approximately 2 m from each adjacent burrow and 2 m away from the enclosure walls. In all, 120 burrows were constructed in fire-suppressed enclosures, and 120 burrows were made in fire-maintained enclosures, totaling 240 burrows for the entire study.



Figure 2. An artificial burrow with a mesh sleeve removed (left) and an auger used to dig artificial burrows (right).

I constructed the artificial burrows using an earth/bulb auger with a 7.3 cm diameter drill bit (STIHL BT 45, STIHL Incorporated, Virginia Beach, VA). The artificial burrows (Fig. 2) were dug into the ground at approximately a forty-degree angle and extended 55.9 cm into the ground. The diameter of the hole (7.6 cm) was larger than needed for juvenile frogs but ensured

the frogs could use them at maturity. The entrance to each burrow was oriented towards the pond based on each enclosure's spatial block position (enclosures in block one = 30°, block two = 80°, block three = 90°, and block four = 140°) because a preliminary survey around Glen's Pond showed natural burrows to be oriented towards the pond, regardless of location. All disturbed soil recovered from the holes was removed from the enclosure or flattened to minimize the risk of attracting fire ants. I observed no increase in the number of fire ant mounds in the enclosures during this experiment, nor were there any cases of fire ants occupying artificial burrows. Each burrow was assigned an individual number and marked with a flag for identification.

I lined each burrow with a sleeve made of fiberglass window screen connected with staples. The sleeves were approximately 50 cm in length and sat just below the topsoil. The artificial burrows were durable enough to withstand the weight of an adult human standing directly overtop without collapsing, even in the semi-sandy soil characteristic of this habitat. No burrows collapsed during this study. On a few occasions, burrows filled completely with soil as the result of heavy rains carrying the soil into the mesh sleeve. This was a slow, gradual process where loose soil was deposited inside the flooded artificial burrow. I believe this was of no concern and carried little risk to the frogs as natural burrows likely endure the same processes, and a frog could easily escape the burrow. The soil was removed from the sleeve when this occurred.



Figure 3. Juvenile dusky gopher frog with a VI alphanumeric tag underneath the skin of its left hind leg

Thirty metamorphs were randomly chosen for release into each enclosure using a stratified random selection, first by date of metamorphosis, then block, and finally enclosure. Prior to release, each individual metamorph was weighed using a spring scale and snout-vent length (SVL) was measured using calipers. Metamorphs were also marked with a fluorescent Visible Implant Alphanumeric tag (VIA tag; Northwest Marine Technology, Shaw Island, WA) inserted under the skin of its left lower hind leg (Richards et al., 1994; Figure 3). Frogs were released into the enclosures on damp nights from 21 – 30 May, mimicking conditions typical of a natural migration away from their pond.

I monitored the frogs' use of the artificial burrows, along with their somatic growth and survival using mark-recapture methods from June 2018 – January 2019. The enclosures were surveyed, and frogs were captured at two-week intervals from 2 June to 12 August, and again at

two-month intervals from 15 October to 4 January. The recapture procedures consisted of artificial burrow surveys, pitfall trap surveys, and transect surveys. All three survey methods were performed twice in each enclosure every sample period.

I surveyed each enclosure twice each sample period, once during the day and again that same night. The surveys conducted during the day began 4 hours prior to sunset and surveys conducted at night began one hour after sunset. I surveyed during the day to maximize recapture rates of individuals inside of burrows, seeking refuge from harsh weather conditions. I surveyed at night to maximize the recapture rate of individuals found outside of burrows, foraging in more favorable weather conditions.

Each survey event, with the exception of the first survey, was performed over the course of four days and nights, one block of enclosures per day. The first survey was conducted over the course of two days and nights, sampling two blocks each day. The order in which enclosures were surveyed was chosen at random each survey.

The artificial burrow survey consisted of removing the artificial burrow's sleeve if a frog was seen inside of the hole, identifying the individual by its VIA tag, and measuring the frog's snout-vent length (SVL) and mass. Once measurements were recorded, the sleeve was placed back inside of the burrow, along with the animal.

Pitfall traps were also used during recapture events to assist in collecting frogs that were actively wandering around the walls of the enclosure. The pitfall traps were activated 4 hours prior to a recapture procedure. Pitfall traps fashioned from 25-liter buckets buried in the soil were placed in each corner ($n=4$) of each enclosure. An unbleached sponge was placed in each pitfall bucket to provide animals with moisture and to use as a floatation device if the bucket accumulated water. To inactivate the pitfall traps after recapture events, a lid was placed on top

of each bucket, and a clay brick was placed on top of the lid to ensure that the lid was secure and that no animals could enter the trap. After measurements were recorded, frogs retrieved from pitfall traps were placed approximately 1 m away from the pitfall bucket.

During each recapture event, I searched for frogs along ten transects per enclosure. Each transect spanned the length of the enclosure. Five evenly-spaced transects ran from the north to the south wall and five ran from the east to the west wall. After measurements of the frog were taken, the animal was returned to the same location.

After the final sampling, an approximately ~1.5 m aperture was created in the wall of each enclosure oriented towards Glen's Pond. This ensured that any mature frogs could easily exit the enclosure for a breeding migration.

Habitat Assessment

I assessed several habitat variables in each enclosure at four locations, each centered 7.07 m from a corner and 5 m out from each of the two adjacent walls. The percent cover of ground vegetation and of litter was assessed using 1-m² quadrats centrally located on each sampling plot. I estimated cover by eye at a height of 1 m using the following categories: live grasses and sedges; live herbs, forbs, and ferns; live vines; live shrubs and hardwood saplings; woody debris (including bark); live pine seedlings; leaf litter (all types); bare ground; and standing dead vegetation (all types). Some observations exceeded 100% due to overlap in this three-dimensional space. Since the frequently-burned habitat had recently experienced a prescribed burn, litter depth was not measured. These samplings were performed on 3 August.

Percent soil volumetric water content (SVWC) was measured once at the center of each of the 4 sampling plots per enclosure using a Fieldscout TDR 300 Soil Moisture Meter with 20 cm rods (Spectrum Technologies, Inc., Plainfield, IL). These measurements were all made on the

same day (within 2 hours) to reduce variation due to weather. I sampled SVWC on 1 August 2018, 2 days after a rain, when the soils had intermediate wetness.

To measure the percentage of canopy cover, I took a hemispherical photograph, using a Canon EO3 fisheye lens (Canon Inc, Ōta, Tokyo, Japan), at the center of each of the four quadrats from 1 m height above the ground. I analyzed these pictures using Gap Light Analyzer software (GLA v.2, Institute of Ecosystem Studies, Millbrook, NY) to compare the canopy cover between habitats. These photographs were captured 4 August 2018 (114 days after the most recent prescribed burn), on a relatively cloudy day to reduce glare.

Finally, I performed natural burrow surveys in every enclosure along two transect lines that each passed through two of the four sample plots used in the ground cover surveys. I recorded natural burrows greater than 1 cm wide and 3 cm in depth within 1 m on either side of the line transect on. These surveys were performed on 2 August and vegetation had increased substantially since the most recent burn.

Arthropod Abundance

I measured the availability of invertebrates as a food source in the fire-maintained and fire-suppressed habitats. Flypaper traps were placed both directly inside and outside of artificial burrows constructed just outside each enclosure, where the traps could not accidentally capture and injure the juvenile frogs inside the enclosures. Samples were collected from fixed sites located approximately 1-2 m away from the middle of each exterior wall of the enclosure. Every exterior wall (excluding the middle, dividing wall) was randomly assigned a sample type each sampling period; burrow, pad, or air. The exterior of each enclosure possessed all 3 treatment groups at any given sampling period. There were four sampling periods (48 traps [16 burrow, 16 pad, and 16 air] x 4 sampling periods = 192 total samples).

All sampling traps in the three treatments had an adhesive surface area of 386.1 cm². Burrow sampling consisted of a sheet of flypaper, measuring 15.2 cm x 25.4 cm, rolled into a cylinder and placed inside the entrance of an artificial burrow, set flush with the top of the organic layer of the soil. The artificial burrow was constructed using the same techniques described in the earlier experiment. Pad sampling consisted of a 15.2 cm x 25.4 cm sheet of flypaper placed on the ground directly in front of the entrance to the artificial burrow. Air sampling consisted of a sheet of flypaper, measuring 15.2 cm x 12.7 cm and with both sides exposed, vertically attached to a small metal rod directly in front of the artificial burrow and positioned approximately 5 cm off the ground. This positioning was to sample invertebrates that a frog on its pad could capture out of the air.

The traps were collected 5 days, or 120 hours, after deployment. The first survey began 16 July and the last survey concluded 5 August. Arthropods were counted and identified to order using a microscope, with the exception of Entognatha (Collembola), which were identified to subclass.

Thermal Variation Assessment

Two separate studies were performed to determine whether temperature varied between the fire-maintained and fire-suppressed habitat. In the first study, temperatures were collected using an infrared thermometer (Lasergrip 1022, Etekcity Corporation, Anaheim, CA). I recorded temperatures from the bottom of artificial burrows, those burrows' corresponding pads, and on the ground approximately 0.3 m away from the artificial burrows. Five artificial burrows were randomly selected for temperature measurements at every enclosure during every survey event. Surveys were performed at sunrise, 1400, and sunset daily for 4 consecutive days (4 - 8 Aug) under mostly sunny weather conditions.

The second study used temperature loggers (iButtons Maxim Integrated, 160 Rio Robles, San Jose, CA) with a 15-minute sampling interval. An iButton was placed at a depth of 35.9 cm below ground, inside the bottom of the centermost artificial burrow within each enclosure containing artificial burrows. Each iButton was enclosed inside two sealed plastic bags to protect the device from water damage. Another set of iButtons was placed in the middle of the same enclosures to record surface temperatures. Each surface iButton was mounted in a housing unit constructed of PVC Tee pipe (11.8 cm in length, 5.6 cm in diameter, 8.5 cm height, and 0.5 cm thick) to shade it and protect it from rain and flooding events. Temperatures were recorded from 10 August (outside of burrows) and 12 August (inside of burrows) through 4 January 2019. I only retrieved useable data from 2 replicate iButtons per treatment combination from 10 August to 19 September 2018 due to equipment issues.

STATISTICAL ANALYSES

Growth

A repeated measures approach using a linear mixed effect model was used to determine whether habitat type (fire-managed versus fire-suppressed) and artificial burrows (present versus absent) affected growth. The model was built with fire regime, burrow presence nested within fire regime, and survey as fixed effects and block, enclosure, and individual frogs as random effects. All analyses except mark-recapture were run in R Studio 3.4.3 (2018). All linear mixed effect models were created using the lmerTest package (Kuznetsova et al., 2017).

Survival and Encounter Probability

Apparent survival (Φ) and detection (p) probabilities were analyzed using a Cormack-Jolly-Seber (CJS) open-population model in the program MARK (White & Burnham, 1999). Time interval lengths were set to reflect the 2-weeks between recapture events and adjusted to reflect the 8-week intervals between the last two recapture periods. I first created a model with all possible combinations of the presence and absence of block and time effects, and associated interactions, on survival and detection. I then created a model assuming both survival and encounter probability varied over time and differed between burn treatments, burrow treatments, and their interaction. I then compared this to a series of reduced parameter models that included fire regime alone, but not burrow treatment, and burrow treatment alone, but not fire regime. For these models, each replicate within a treatment was treated as part of the same sample population.

For all models created in program MARK, \hat{c} was adjusted to account for any over- or under-dispersion bias in the observed data. To calculate \hat{c} , a bootstrapped goodness-of-

fit (GOF) was performed on the most highly parameterized model. The observed deviance of that model was divided by the expected deviance to calculate the adjusted \hat{c} . All models with a quasi-likelihood *Akaike Information Criterion* (ΔQAICc) < 2 were considered as having some support; however, model rank was still considered.

Habitat Assessment

A principal components analysis was performed on the habitat variables. Variables for each enclosure were averaged and differences in individual habitat variables between fire-suppressed and frequently-burned habitat were examined using T-tests. Holm's sequential Bonferroni procedure was used to adjust α level in the vegetation variables (Holm, 1979).

Arthropod Availability

Differences in arthropod abundance between fire-suppressed and frequently-burned enclosures and among sampling methods were tested with a repeated measures approach using a linear mixed effect model with spatial block, enclosure, and sample date as random effects. Data were combined for each pair of enclosures (with and without artificial burrows) within a spatial block and treated as a single unit of observation in this analysis. I performed post-hoc t-tests to compare arthropod counts between burned and unburned habitat for five selected taxon/sampling method combinations.

Thermal Variation Assessment

Temperatures sampled with laser thermometers were examined for differences in mean temperatures between habitat type for each individual temperature location (burrow, pad, and ground), with sample dates (sampling period) as replicates, using t-tests. iButton temperatures were first separated and averaged by time of day (day or night), then averaged by date (month) using individual enclosures as replicates. Mean temperatures were then examined using a

repeated measures approach using a linear mixed effect model, with burn regime, iButton location (inside vs outside artificial burrow), time of day (day vs night), and month as fixed effects and individual enclosures as a random effect. Similarly, daily maximum and nightly minimum temperatures were separated and averaged by date (month) using individual enclosures as replicates.

RESULTS

Growth

Fire regime, presence or absence of artificial burrows (tested as an interaction with fire regime because of the split plot design), survey date, the interaction of survey date with fire regime and with artificial burrows, and block significantly affected mass and SVL (Tables 1-2). Gopher frogs recaptured in the frequently-burned habitat with artificial burrows showed the greatest overall increases in both mass and snout-vent length (Figs 4-5). Frogs in frequently-burned enclosures that were supplemented with artificial burrows increased in mean mass (\pm SE) from 3.23 ± 0.20 g to 15.08 ± 0.29 g (Fig. 4) and in mean SVL from 32.73 ± 0.55 mm to 49.24 ± 0.69 mm (Fig. 5). Frogs recaptured in the fire-suppressed habitat without artificial burrows had the lowest growth increasing in mean mass from 3.20 ± 0.20 g to 4.75 ± 1.08 g (Fig. 4) and in mean SVL from 32.65 ± 0.56 mm to 39.81 ± 2.07 mm (Fig. 5).

Average growth in frequently-burned habitat without artificial burrows and fire-suppressed habitat with artificial burrows was similar and intermediate to that in the other treatments. The mean mass of frogs in frequently-burned habitat without artificial burrows increased from 3.20 ± 0.20 g to 6.00 ± 0.79 g (Fig 4), while their SVL increased from 32.68 ± 0.56 mm to 41.12 ± 1.54 mm (Fig 5). Frogs in fire-suppressed habitat with artificial burrows increased in mass from 3.46 ± 0.20 g to 6.98 ± 0.56 g (Fig 4) and in SVL from 33.36 ± 0.55 mm to 41.69 ± 1.03 (Fig 5).

Table 1. Repeated measures linear mixed effect model results for mass and SVL. Burrows represents the presence or absence of artificial burrows.

Effects		MS	Df _{num}	Df _{den}	F	P
Fire Regime	Mass	102.23	1	14.01	111.313	< 0.0001
	SVL	82.11	1	12.18	26.517	0.0002
Survey	Mass	79.38	8	903.24	86.433	< 0.0001
	SVL	550.96	8	788.35	177.926	< 0.0001
Fire Regime x Burrows	Mass	39.65	2	27.67	43.167	< 0.0001
	SVL	31.46	2	20.76	10.160	0.0008
Fire Regime x Survey	Mass	42.62	8	877.94	46.404	< 0.0001
	SVL	66.12	8	772.24	21.352	< 0.0001
Fire Regime x Burrows x Survey	Mass	10.34	16	897.83	11.262	< 0.0001
	SVL	10.80	16	785.5	3.489	< 0.0001

Table 2. ANOVA-like table for random-effects on mass and SVL: Single term deletions. Npar is the number of parameters for each model, log-Lik is the log-likelihood for each model, AIC is *Akaike information criterion*, and LRT is the likelihood ratio test for each model.

Random Effects		npar	log-Lik	AIC	LRT	Df	Pr(>Chisq)
ID x (Enclosure x Block)	Mass	39	-2002.1	4082.1	265.69	1	< 0.0001
	SVL	39	-2950.7	5979.4	505.73	1	< 0.0001
Enclosure x Block	Mass	39	-1869.7	3817.3	0.90	1	0.3429
	SVL	39	-2698.1	5474.3	0.57	1	0.4519
Block	Mass	39	-1871.6	3821.2	4.83	1	0.0280
	SVL	39	-2702.0	5482.0	8.32	1	0.0039

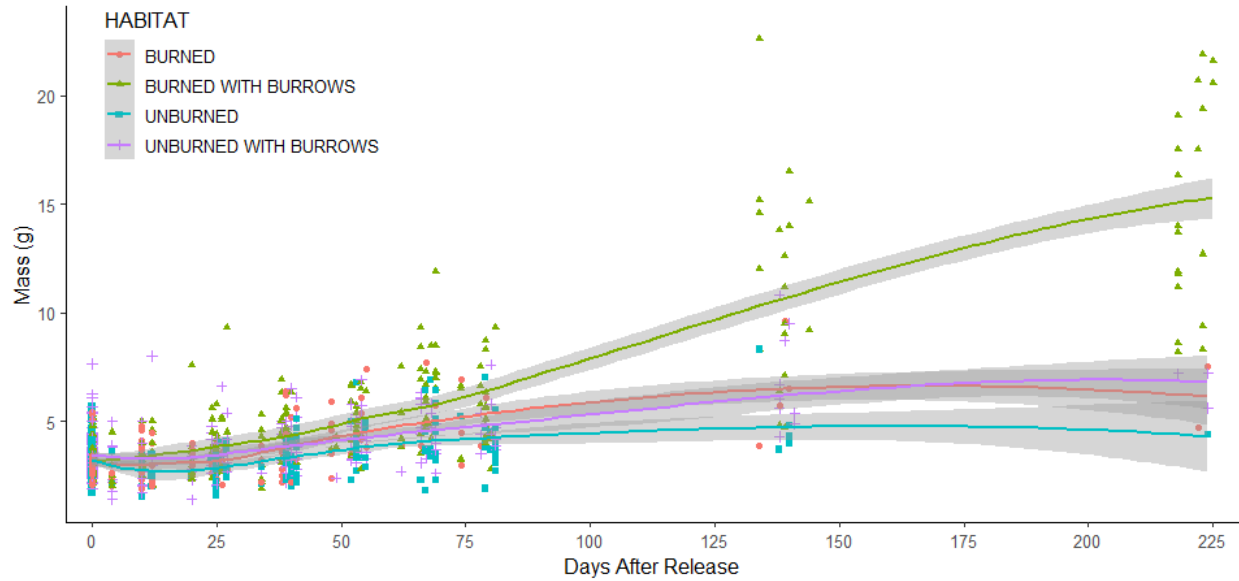


Figure 4. Changes in least square (ls) mean mass over the course of the experiment for all treatments with 95% confidence intervals (shaded).

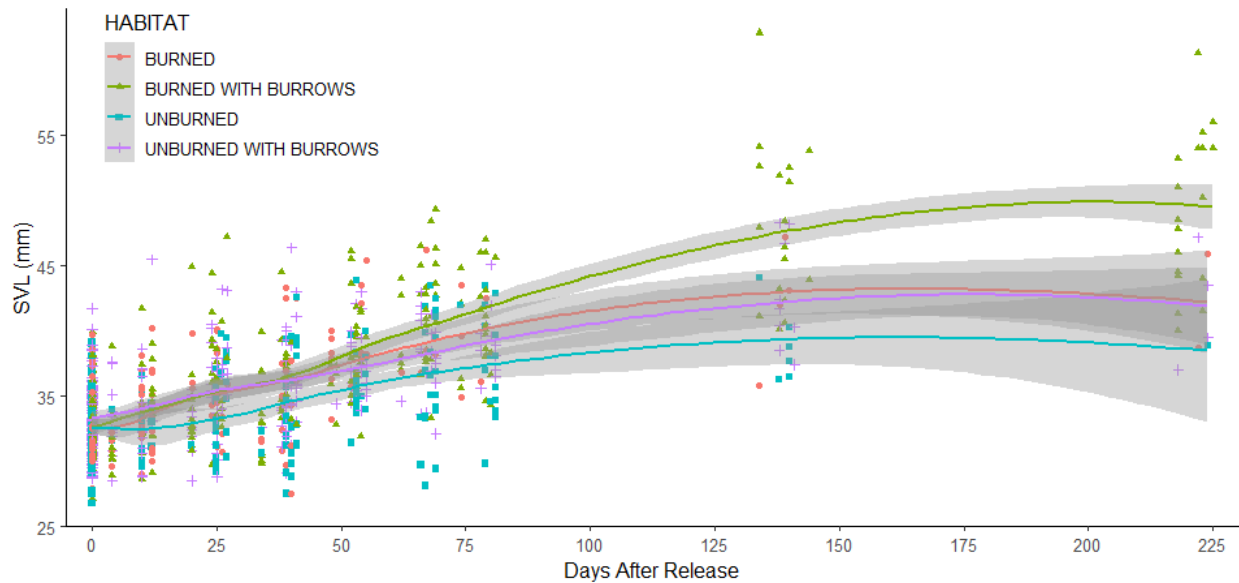


Figure 5. Changes in ls mean snout-vent length over the course of the experiment for all treatments with 95% confidence intervals (shaded).

Survival and Encounter Probability

In a preliminary test for block effects, the top model had survival as constant among blocks and detection dependent on an interaction between the block and time (Table 3). A second supported model had survival dependent on block and detection dependent on an interaction between block and time (Table 3). Other models had poorer fits (all $\Delta\text{QAICc} > 9$). Estimated mean survivorship was constant at 85% in the best-fitting model and varied only from 83%-89% among blocks in the second best-fitting model. I pooled data for all the blocks for subsequent mark-recapture analyses.

Table 3. CJS models examining the effects of block and sampling period (time) on the apparent survival (Φ) and detection (p) probabilities of juvenile *R. sevosia*. Models were considered as having some support if ΔQAICc (quasi-likelihood Akaike information criterion) was < 2 . Models with a weight < 0.000 are excluded from this table.

Model	QAIC _c	ΔQAICc	Weight	Parameters	QDeviance
Φ (.) p (block x time)	3521.03	0.000	0.518	33	519.88
Φ (block) p (block x time)	3521.20	0.176	0.474	36	513.66
Φ (time) p (block x time)	3530.20	9.173	0.005	40	514.07
Φ (block x time) p (block)	3531.93	10.899	0.002	36	524.38
Φ (block x time) p (.)	3535.59	14.561	0.000	33	534.44

For models examining how fire regime, artificial burrow availability, and sampling period affected survival and encounter probabilities, the best-fitting model (QAIC_c Weight = 0.94490) had survival dependent on experimental treatment combination and detection dependent on the interaction of treatment combination and time (Table 4). Other models had poorer fits (all $\Delta\text{QAICc} > 6$). Fire-maintained habitat with artificial burrows had a significantly greater survival probability than any other treatment (Fig. 6). The other treatments all had similar

survival probabilities. Reduced models that included fire regime but not burrow treatment, or burrow treatment but not fire regime, had little support (Table 4).

Table 4. CJS models examining the effects of burn regime, artificial burrow treatment, and sampling period (time) on the apparent survival (Φ) and detection (p) probabilities of juvenile *R. sevosia*. Group indicates the combination of burn regime and burrow treatment except where otherwise noted. Models were considered as having some support if ΔQAICc (quasi-likelihood Akaike Information Criterion) was < 2 .

Model	QAIC _c	ΔQAIC_c	Weight	Parameters	QDeviance
Φ (group) p (group x time)	3359.47	0.000	0.945	36	480.23
Φ (group) p (group)	3365.70	6.223	0.042	8	544.81
Φ (group) p (time)	3369.20	9.729	0.007	12	540.16
Φ (group) p (.)	3369.68	10.207	0.006	5	554.87
Φ (.) p (group x time)	3379.88	20.401	0.000	33	507.03
Φ (time) p (group x time)	3382.15	22.680	0.000	40	494.32
Φ (group x time) p (group)	3382.20	22.729	0.000	36	502.96
Φ (group x time) p (.)	3388.74	29.264	0.000	33	515.89
Φ (group) p (group x time) ^a	3391.61	32.136	0.000	18	550.22
Φ (group x time) p (time)	3392.39	32.920	0.000	40	504.56
Φ (group) p (group x time) ^b	3396.32	36.846	0.000	18	554.93
Φ (group x time) p (group x time)	3397.12	37.644	0.000	64	456.39
Φ (.) p (group)	3404.86	45.382	0.000	5	590.04
Φ (time) p (group)	3405.77	46.298	0.000	12	576.73
Φ (.) p (time)	3417.23	57.758	0.000	9	594.31
Φ (.) p (.)	3421.03	61.557	0.000	2	612.26
Φ (time) p (.)	3421.56	62.087	0.000	9	598.64
Φ (time) p (time)	3424.52	66.048	0.000	16	588.26

^a Model considers presence or absence of artificial burrows as groups.

^b Model considers burned or unburned habitat as groups.

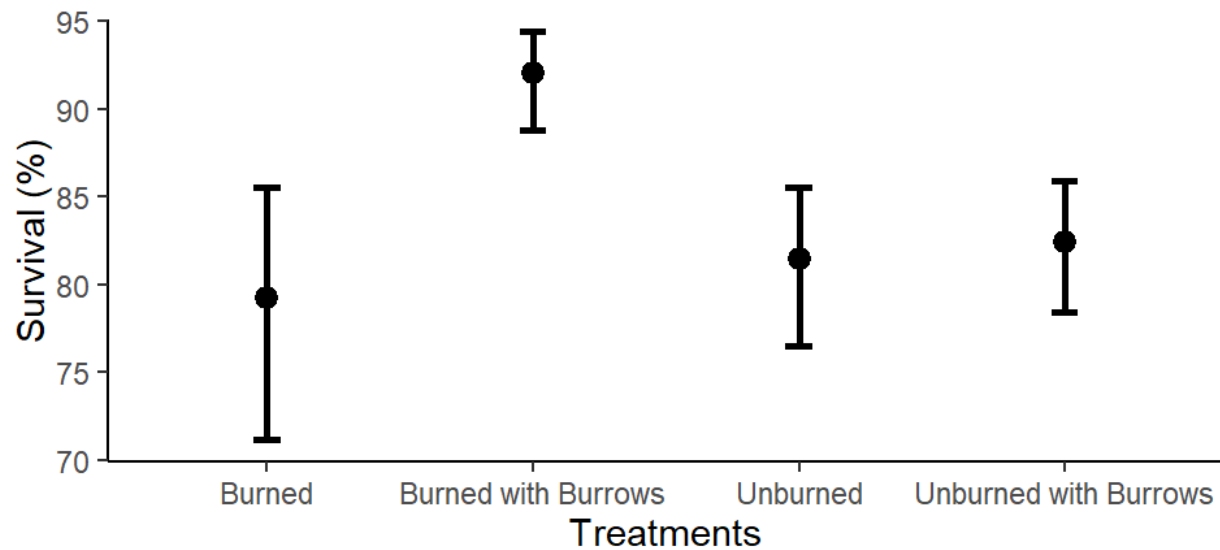


Figure 6. Survival estimates with 95% confidence intervals for each treatment combination, using the most likely model (Φ [group] p [group x time]).

Habitat Assessment

The PCA provided evidence that several related variables were characteristic of each habitat and grouped sampling sites accordingly (Figure 7). PC1 accounted for 48.9% of the variation among habitat variables with percent vines, shrubs, coarse woody debris, leaf litter, and canopy coverage having positive scores and grass, herbs, pine seedlings, bare ground, standing dead vegetation, and soil moisture having negative scores (Table 5). All fire-suppressed sampling sites had positive scores for PC1 whereas all frequently-burned sampling sites had negative scores for PC1 (Fig. 7).

Soil moisture and the percent cover of bare ground, herbs, and grass were greater in frequently-burned habitat than in the fire-suppressed habitat ($p \leq 0.0128$; Figure 8). Twice the number of natural burrows were found in the frequently-burned habitat (altogether totaling 50) than in the fire-suppressed habitat (altogether totaling 25), with the natural logarithm of burrows

per enclosure differing significantly between habitats ($p < 0.0376$; Figure 8). The percent cover of canopy, shrubs, leaf litter, and coarse woody debris was greater in the fire-suppressed habitat than in the frequently-burned habitat ($p \leq 0.0135$; Figure 9). Percent cover of standing dead vegetation ($p = 0.2800$), vines ($p = 0.1170$), and pine seedlings ($p = 0.8800$) did not differ significantly between habitats.

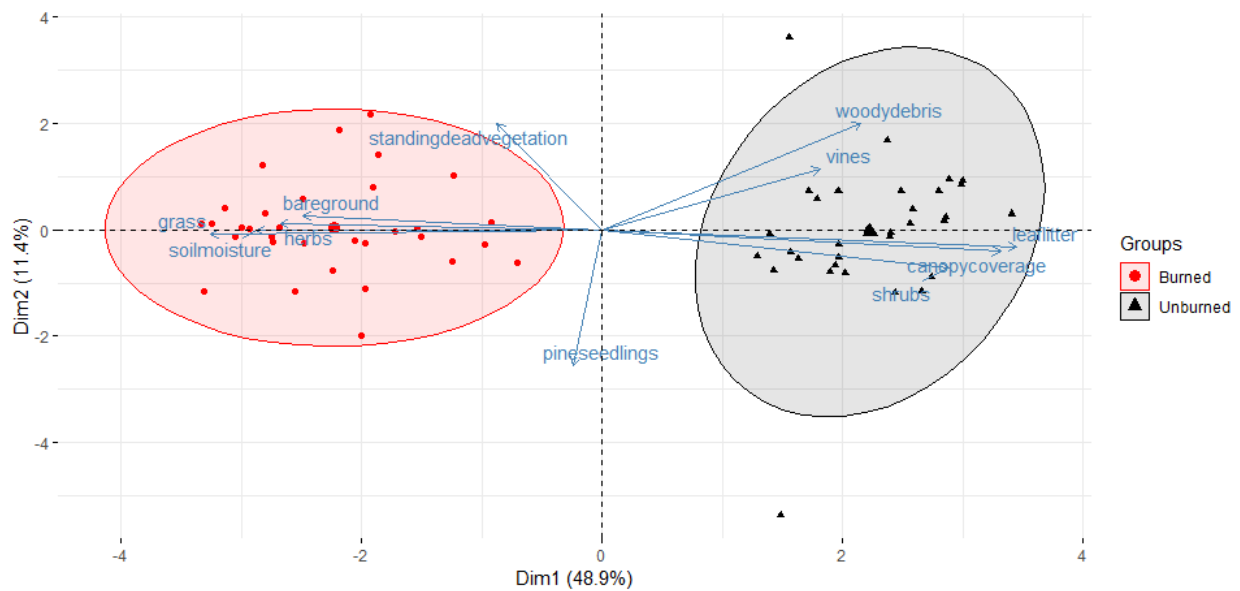


Figure 7. Distribution of the first two principal components of the environmental variables. Labeled arrows represent the direction of the variables, length indicates standard deviation, and cosine of the angle between variables indicates correlation. Red points represent fire-maintained plots and black points represent fire-suppressed plots.

Table 5. Loadings for environmental variables for the first two principal components. Environmental variables were measured as percentages.

	PC 1	PC 2
Grass	-0.888	-0.021
Herbs	-0.731	0.035
Vines	0.496	0.315
Shrubs	0.787	-0.198
Woody Debris	0.588	0.547
Pine Seedlings	-0.064	-0.699
Leaf Litter	0.942	-0.085
Bare Ground	-0.678	0.075
Standing Dead Vegetation	-0.239	0.550
Soil Moisture	-0.785	-0.004
Canopy Coverage	0.905	-0.111

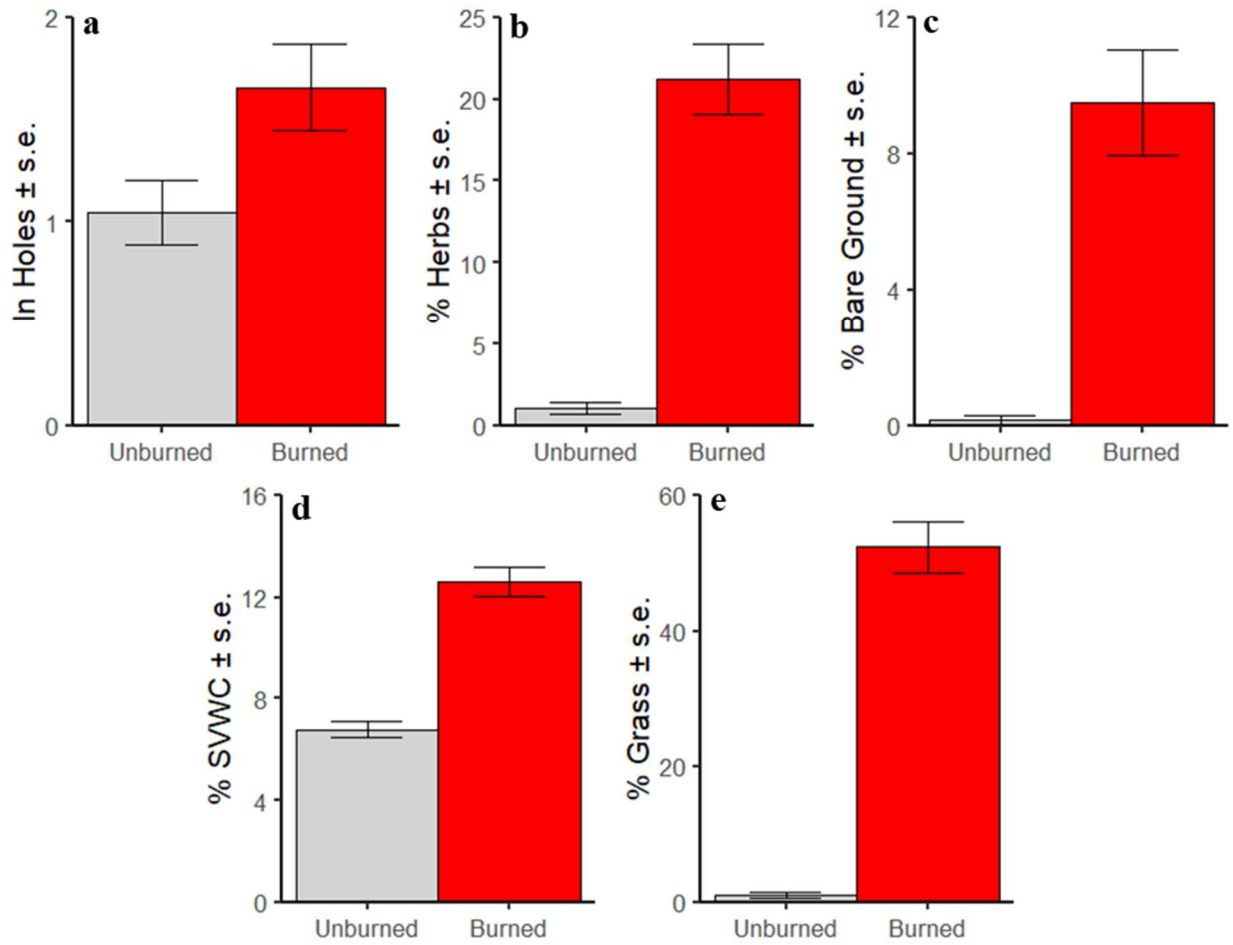


Figure 8. Environmental characteristics (mean \pm s.e.) of fire-maintained habitat compared to fire-suppressed habitat including a) ln number of natural holes ($p=0.0376$) and percent b) cover of herbs ($p=0.0003$), c) cover of bare ground ($p=0.0128$), d) soil moisture by volume (SVWC, $p<0.0006$), and e) cover of grass ($p<0.0002$).

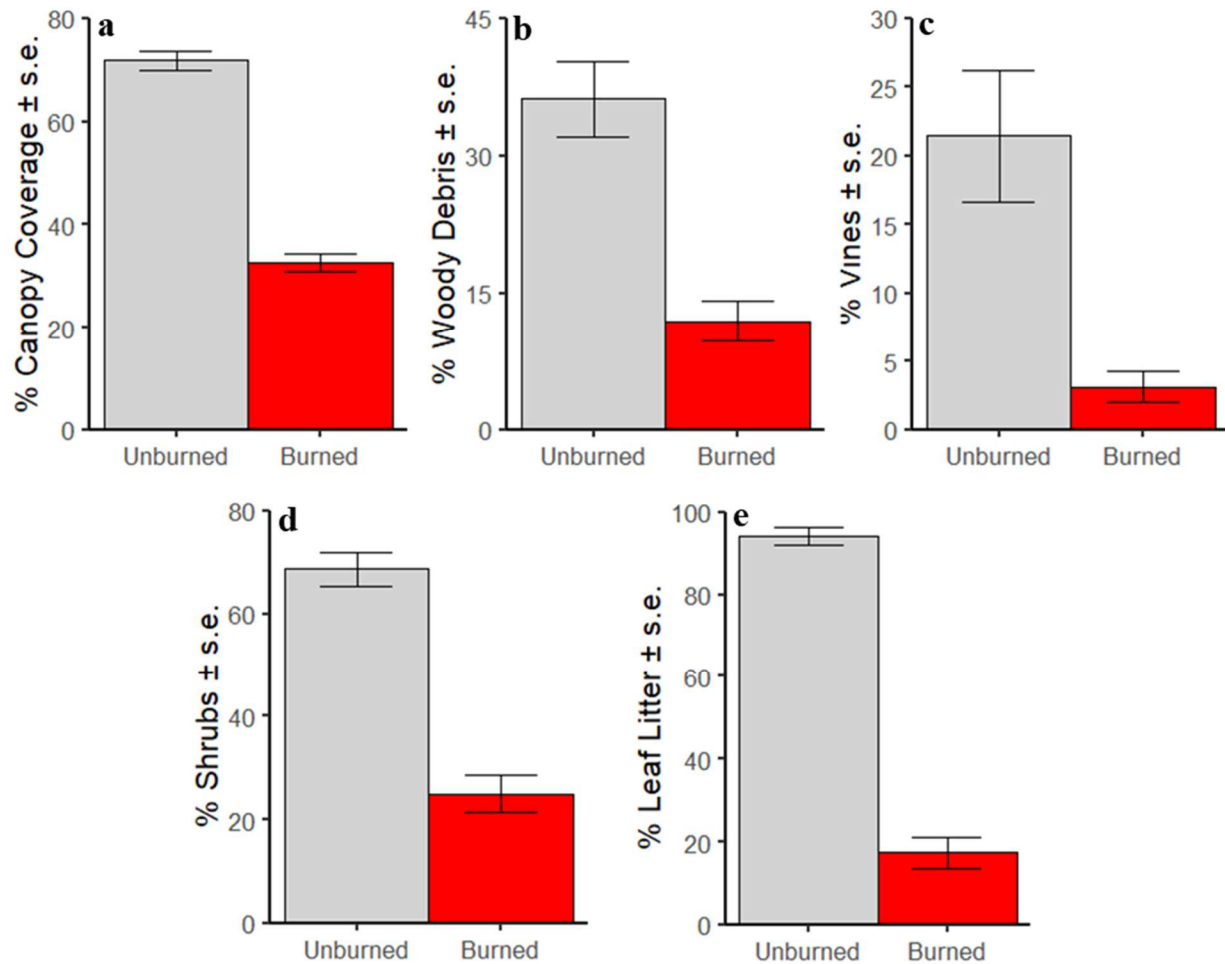


Figure 9. Environmental characteristic (mean \pm s.e.) of fire-suppressed habitat compared to fire-maintained habitat, including percent cover of a) canopy ($p < 0.0001$), b) woody debris ($p = 0.0135$), c) vines ($p = 0.1170$), d) shrubs ($P < 0.0002$), and e) leaf litter ($p < 0.0001$).

Arthropod Abundance

The overall total of arthropods sampled in frequently-burned and fire-suppressed habitats, regardless of sample location and sample time, differed by 5 arthropods (frequently-burned $N = 2634$ and fire-suppressed $N = 2629$). There was no significant difference between habitats in the mean number of arthropods captured (Table 6). There were significant differences in arthropod capture numbers among flypaper locations and dates, and a significant effect of the interaction

between flypaper location and habitat on capture numbers (Table 6). Captures were lower in the burrows than in the other two locations (Fig. 10). Captures were highest in the air in the frequently-burned habitat, but highest on the pad in the fire-suppressed habitat (Fig. 10).

Table 6. Repeated measures linear mixed effect model results for arthropod abundance.

Main Effects	MS	Df _{num}	Df _{den}	F	P
Paper Location	35944.04	2	66	22.5813	< 0.0001
Habitat	0.18	1	6	0.0001	0.9919
Date	14046.34	3	66	8.8244	< 0.0001
Paper Location x Habitat	7932.17	2	66	4.9833	0.0096
Paper Location x Date	1918.13	6	66	1.2050	0.3149
Habitat x Date	724.37	3	66	0.4551	0.7146
Paper Location x Habitat x Date	330.53	6	66	0.2070	0.9734

Table 7. Anova-like table for random-effects on arthropod abundance: Single term deletions.

Random Effects	npar	logLik	AIC	LRT	Df	Pr(>Chisq)
Date x (Enclosure x Block)	27	-385.38	824.76	0.0000	1	1.0000
Enclosure x Block	27	-385.61	825.22	0.4631	1	0.4962
Block	27	-385.38	824.76	0.0000	1	1.0000

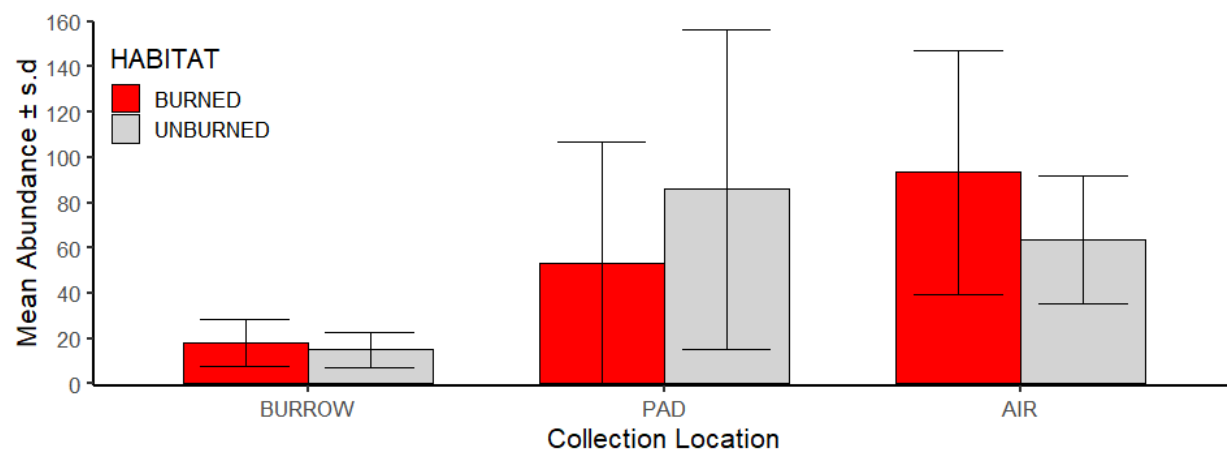


Figure 10. Mean number of arthropods captured (\pm s.d.) per each enclosure pair for the three treatment locations in frequently-burned (red) and fire-suppressed (grey) habitats.

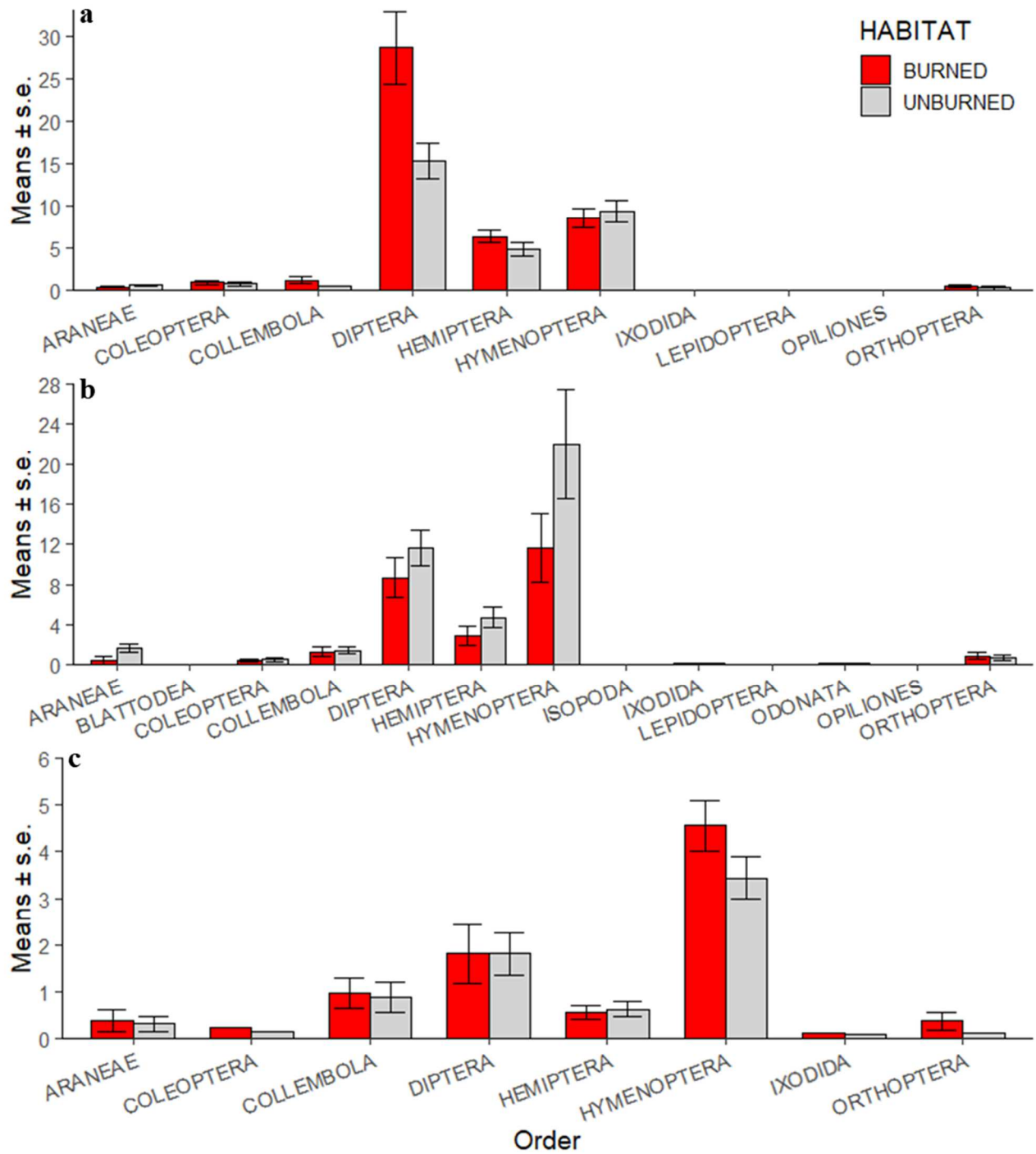


Figure 11. Mean (\pm s.e.) number of invertebrate captures by taxa per individual sample collected from a) air, b) pad, and c) burrow locations. Red bars represent fire-maintained habitat and grey bars represent fire-suppressed habitat.

Invertebrate taxa captured were similar within sampling locations among the two habitats, with a single exception (Fig. 11). Dipterans captured in the air were significantly greater in the frequently-burned than in fire-suppressed habitat ($P = 0.005$; Fig. 11a).

Thermal Variation Assessment

The infrared laser thermometer temperature readings for temperatures inside burrows were greater in frequently-burned habitat by 1.17°C (sunrise), 1.64°C (day), and 1.54°C (sunset) than in fire-suppressed habitat (all $p < 0.0001$; Figure 12). Temperatures of pads located in frequently-burned habitat were also greater by 0.73°C (sunrise), 2°C (day), and 0.82°C (sunset) than those of pads located in the fire-suppressed habitat (all $p \leq 0.008$; Figure 12). Ground surface temperatures were 0.44°C greater in the frequently-burned habitats than in the fire-suppressed habitats only during sunrise sampling ($p = < 0.0001$; Figure 12). Day and sunset ground surface temperatures did not vary significantly between the two habitats ($p \geq 0.082$).

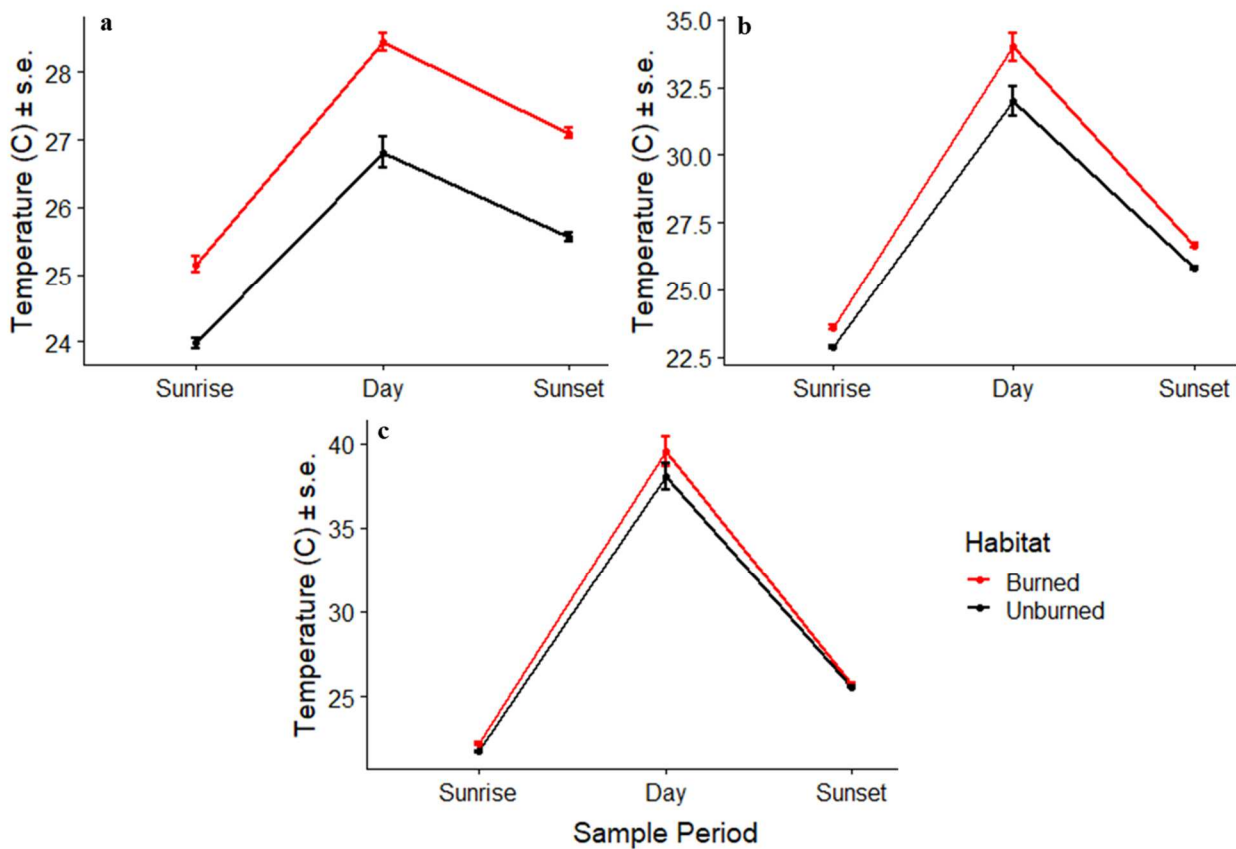


Figure 12. Mean (\pm s.e.) laser-sampled temperatures a) inside artificial burrows, b) on pads, and c) on the ground surface at sunrise, at midday, and at sunset in frequently-burned (red) and fire-suppressed (black) habitats.

Table 8. Repeated measures linear mixed effect model results for iButton means. Placement refers to iButton placement inside vs outside of burrows and time refers to time of day (day vs night).

Main Effects	MS	Df _{num}	Df _{den}	F	P
Habitat	64.30	1	43.76	6.0489	0.0179
Placement	425.96	1	3520.19	40.0731	< 0.0001
Time	1408.36	1	3788.81	132.4947	< 0.0001
Month	15570.48	5	3736.47	1464.8253	< 0.0001
Habitat x Placement	30.73	1	3520.19	2.8907	0.0892
Habitat x Time	29.43	1	3788.81	2.7692	0.0962
Placement x Time	464.55	1	3788.81	43.7038	< 0.0001
Habitat x Month	24.65	5	3736.47	2.3194	0.0410
Placement x Month	180.05	5	3629.75	16.9384	< 0.0001
Time x Month	15.67	5	3788.82	1.4738	0.1949
Habitat x Placement x Time	0.53	1	3788.81	0.0503	0.8225
Habitat x Placement x Month	2.91	5	3629.75	0.2736	0.9277
Habitat x Time x Month	14.40	5	3788.82	1.3551	0.2381
Location x Time x Month	22.04	5	3788.81	2.0736	0.0657
Habitat x Placement x Time x Month	0.77	5	3788.81	0.0728	0.9963

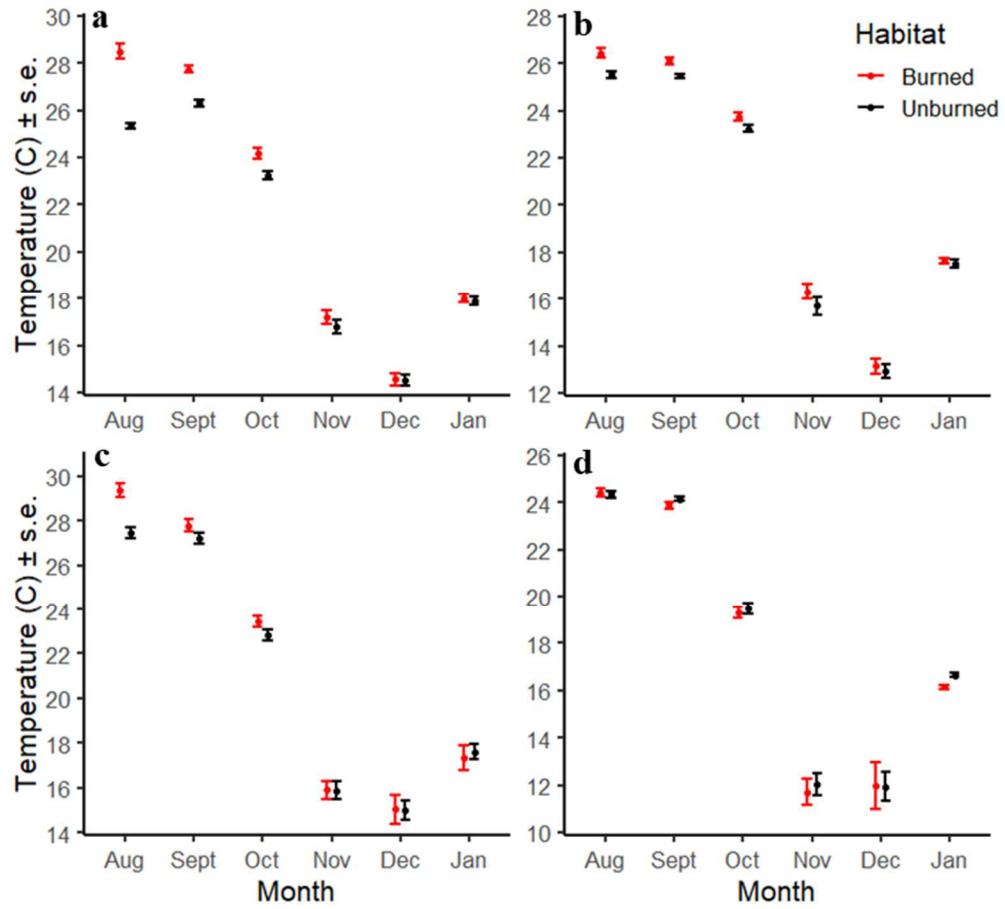


Figure 13. Mean temperatures (± s.e.) collected using iButtons in fire-maintained (red symbols) and fire-suppressed (black symbols) habitat, including a) daily temperatures inside burrows, b) nightly temperatures inside burrows, c) daily ground surface temperatures, and d) nightly ground surface temperatures.

Table 9. Mean daily maximum and minimum temperatures (C) and ranges from inside artificial burrows and the ground surface per month from 8 August 2018 – 3 January 2019.

		Inside Burrows		Ground Surface	
	Fire Regime	Max - Min	Range	Max - Min	Range
Aug	Burned	33.3 - 25.6	7.7	35.7 - 22.7	13.0
	Unburned	25.8 - 25.1	0.6	32.0 - 22.8	9.2
Sept	Burned	30.9 - 25.1	5.8	32.8 - 22.6	10.1
	Unburned	28.7 - 24.8	3.9	31.2 - 22.9	8.3
Oct	Burned	25.7 - 23.1	2.6	30.4 - 18.0	12.5
	Unburned	23.9 - 22.8	1.1	28.6 - 17.9	10.6
Nov	Burned	18.8 - 15.6	3.2	20.5 - 10.3	10.2
	Unburned	18.3 - 14.9	3.4	19.6 - 10.6	9.1
Dec	Burned	16.8 - 12.4	4.4	18.9 - 10.4	8.5
	Unburned	16.9 - 12.0	4.9	18.4 - 10.0	8.4
Jan	Burned	19.0 - 16.8	2.2	19.4 - 15.3	4.1
	Unburned	19.1 - 16.5	2.6	19.4 - 15.9	3.6
\bar{x}	Burned		4.31		9.73
	Unburned		2.75		8.20

Habitat, iButton placement, time of day, and month significantly affected mean temperature (all $P < 0.018$; Table 8). The interactions between iButton placement and time, habitat and month, and iButton placement and month were also significant (all $P \leq 0.041$; Table 8). Data collected from iButtons revealed trends similar to those collected using a laser thermometer. Temperatures inside artificial burrows were warmer in fire-maintained habitat than in fire-suppressed habitat from August through October both day and night (Figure 13). Burrow temperatures from November through January showed little variation between habitats. Samples collected on the ground surface during the day were substantially greater in the fire-maintained habitat only in August. Nightly ground surface temperatures were warmer in fire-suppressed habitats in January. All other ground surface temperature means showed little variation between

habitats. Temperatures inside burrows were cooler than those on the surface during the hottest parts of the day and warmer during the coolest parts of the night (Table 9). Average minimum temperatures inside burrows were always warmer in burned habitat. Average maximum temperature inside artificial burrows were warmer in burned habitat with the exception of December and January (Table 9).

DISCUSSION

I demonstrated that terrestrial habitat management influences the growth and survival of juveniles of a critically endangered amphibian, the dusky gopher frog. My key results were that 1) growth was higher in a fire-maintained landscape than in a fire-suppressed landscape, 2) augmenting refuge density using artificial burrows increased growth, and 3) integration of both fire-maintenance and burrow augmentation increased survival in these amphibians. While some work has been done on the survival of dusky gopher frogs in terrestrial habitats (Richter & Seigel, 2002; Roznik & Johnson, 2009a), this is, to my knowledge, the first study examining how terrestrial habitat management affects dusky gopher frogs' growth. I am also not aware of any previous studies that demonstrated an effect of artificial burrows on growth for any animal. Determining species-specific ecological requirements and resource needs, along with their consequences, is paramount in recovery operations for species at risk.

Several studies have found that *R. sevosia* and its relatives *R. capito* and *R. areolata* select frequently-burned habitats over fire-suppressed habitat, and attribute this preference to open canopies and greater burrow densities (Humphries & Sisson, 2012; Tupy, 2012; Roznik & Johnson 2009a; Roznik & Johnson, 2009b; Roznik et al., 2009; Williams et al., 2012). I found a higher density of natural burrows in the frequently-burned habitat than in fire-suppressed habitat, consistent with the findings of similar studies (Roznik, 2009b; Thurgate, 2006; Tupy, 2012). The mean number of natural burrows or holes found in fire-maintained enclosures, $6.25/60 \text{ m}^2$ ($0.1/\text{m}^2$), was exactly double of those found in the fire-suppressed habitat, $3.13/60 \text{ m}^2$ ($0.05/\text{m}^2$). Artificial burrow densities experimentally provided were similar to those found during surveys of natural burrows within fire-maintained enclosures, $30/225 \text{ m}^2$ ($0.13/\text{m}^2$). Both natural and

artificial burrows likely helped facilitate growth by providing additional thermally stable refuges from high daytime temperatures and low nighttime temperatures (Pike & Mitchell, 2013; Heemeyer et al., 2012). Buffered from extreme temperature fluctuations inside burrows, frogs would likely have increased opportunities to maintain their body temperature at the optimum for physiological processes (Stevenson, 1985; Pike & Mitchell, 2013). This optimum is not known for gopher frogs; however, in this study juvenile gopher frogs were observed outside of burrows at minimum temperature of 19.1 °C and a maximum of 36.7 °C. Comparatively, *Rana aereolata* in Indiana have been observed outside of their burrows at minimum and maximum temperatures between 12 - 20.3 °C (Engbrecht & Lannoo, 2012). Shelters can also decrease evaporative water loss in amphibians (Andrade & Abe, 1997). Burrows, especially in the fire-maintained habitat, likely improve water retention rates.

The results of this study point to differences between habitats in mean temperatures as another possible mechanism that affected growth. The forest structure and open canopy of the fire-maintained habitat allowed more solar radiation to reach the understory than in fire-suppressed habitat. This probably led to the higher environmental temperatures these frogs experienced. Higher environmental temperatures found in the frogs' preferred fire-maintained habitat likely increased growth because they increased physiological performance in these animals (Huey, 1991). It is well established for amphibians or any ectothermic organism that physiological processes are dependent upon the temperature of the environment. Physiological processes, especially growth, benefit from higher environmental and body temperatures in these ectothermic organisms (Turner, 1960, Lillywhite et al., 1973; Huey, 1982). Juvenile *Litoria aurea* raised under controlled temperatures of 15°C, 22°C, and 28°C were found to grow and mature the fastest at 28°C (Browne & Edwards, 2003). Optimal temperature ranges are unknown

for *R. sevos*a but are likely reached quicker when the frogs have access to plenty of sunlight and heat under the open canopies offered in the fire-maintained habitat. Cool burrows for refuge under extreme heat are also more plentiful in this habitat, facilitating behavioral thermoregulation (Stevenson, 1985; Pike & Mitchell, 2013). When temperatures are optimal, physiological processes such as digestion and metabolism are maximized, and more energy can be allocated towards growth in juveniles and towards reproduction in adults (Lillywhite et al., 1973; see Pough et al., 1992). Warmer temperatures in the fire-maintained habitat may also help reduce prevalence of *Batrachochytrium dendrobatidis* (Bd) and the risk of chytridiomycosis (Piotrowski et al, 2004; Berger et al, 2004; Rowley & Alford, 2013), further increasing frog growth and survival. Heliothermic activity, such as basking, could reduce the risk of Bd and open canopy habitats would make this process more efficient (Woodhams et al., 2003; Richards-Zawacki, 2010; Kinney et al., 2011).

Survival per recapture event (2-week intervals) had the highest estimated mean at 92 % in fire-maintained habitat with artificial burrows, followed by fire-suppressed habitat with artificial burrows at 82 %, fire-suppressed habitat with no added burrows at 81 %, and fire-maintained habitat with no added burrows at 79 %. The experimental enclosures, and the limitation on migrations that they imposed, may have increased the survival of juvenile *R. sevos*a in my study compared to that of free-ranging frogs. Roznik & Johnson (2009a) found a much higher rate of mortality in newly metamorphosed Carolina gopher frogs that migrated from ponds, with only 12.5 % surviving their first month, due mostly to predation and vehicle deaths, highlighting some of the risks associated with migrations. Locating a burrow is likely an energetically costly activity as well. A high density of refuges likely improves growth by reducing energetic costs associated with locating burrows. Once a juvenile locates a burrow then risk of mortality likely

decreases (Roznik & Johnson, 2009a; Heemeyer, 2011). The increased juvenile survival and growth I observed with the combination of prescribed fire and burrow addition would likely benefit populations by facilitating recruitment of reproductive members.

The results of my habitat assessments were consistent with those of similar studies in gopher frog habitat (Roznik, 2009b; Thurgate, 2006; Tupy, 2012). There was less soil moisture found in the unburned habitat than in the fire-maintained habitat which may be explained by increased transpiration rates from the high density of shrubs and woody plants. The higher soil moisture content associated with the frequently-burned sites may help mitigate the effects of evaporative water loss and improve rehydration rates (Tracy, 1976), allowing frogs to spend more time away from burrows foraging.

As is characteristic of frequently-burned habitat, significantly greater percentages of canopy openness, bare ground, grass, and herbs were observed in these enclosures, with lesser shrub coverage. Modifications to the forest structure brought with fire may make movements easier for frogs than in dense, unburned sites (Denton & Beebee, 1994) while still providing plenty of temporary refuge such as grass clumps (Richter et al., 2001). This would facilitate foraging and migration movements, reducing metabolic expenses, and ultimately increase growth.

There was little evidence that foraging resources differ significantly between these frequently-burned and fire-suppressed habitats. There are conflicting views in the literature as to how arthropod composition and abundance is influenced after prescribed burns and whether there is an effect of fire frequency (Chitwood et al., 2017; New, 2014; Swengel, 2001). The response of arthropods to fire disturbance is highly complex, with time since fire, fire frequency, fire intensity, seasonality, species life history, and species life stage to consider (New, 2014).

Fire may decrease the abundance of arthropod species dependent on leaf litter but increase that of pyrophilous insects and those attracted to herbaceous growth, and leave some communities unchanged (New, 2014; DeSouza et al., 2003). Arthropod densities were similar in the two habitats, suggesting that food availability was an unlikely explanation for the differences in growth between habitats. These results were consistent with those of a previous comparison in the same study sites (Tupy, 2012). I examined only the abundances of arthropods, however, not their nutritional quality or the match between prey availability and any prey selectivity juvenile gopher frogs might exhibit. The dusky gopher frog's diet is not well determined but includes coleopterans (Netting and Goin, 1942) and is likely similar to that of *R. capito*, which consists of small toads, Coleopterans, Hemipterans, Orthopterans, Araneae, and other invertebrates (Dickerson, 1906; Carr, 1940).

The arthropods captured may have been influenced by an edge effect from the placement of the sample traps 1 to 2 m away from the exterior of the enclosure walls. The edges of the enclosures were maintained to ensure that no vegetation was physically touching or next to the walls. This was 1) to safeguard against frogs using the vegetation as ladders to escape the enclosures and 2) to reduce the chance that fire would damage the walls of the enclosures during prescribed burns. Captures may have also been increased by the flypaper's yellow color, because yellow attracts some insects. Captures might have decreased after rains because moisture temporarily decreased the adhesive properties of the "waterproof" flypaper, though initial tests showed that the flypaper regained strength after drying. The biology of arthropods suggests that the effect of damp flypaper was not substantial in estimating total densities, as arthropods are less likely to be active during precipitation.

The use of artificial burrows or cavities for studying wildlife provides a framework that facilitates observation and data collection. In enclosures with artificial burrows available, 54% of all recaptured animals were found inside an artificial burrow. My use of mesh sleeves for recapture in this study was, to my knowledge, a novel method for amphibian retrieval. This method, as an alternative to reaching one's hand in a burrow, is a safer (for both animal and collector) and more reliable method of retrieval. These sleeves are also highly permeable and likely did not hinder water drainage of the burrows. The artificial burrows used in this study showed no signs of decay at the conclusion of the experiment, although similar artificial burrows may have lesser longevity in more sandy soils.

During sleeve removal, I would also periodically remove excess leaf litter and soil from artificial burrows. Removing materials from within artificial burrows may negatively influence burrow reuse in burrowing owls (*Athene cunicularia*; Riding & Belthoff, 2015). It is possible that removing excess leaf litter and soil could influence an individual frog's ability to recognize or determine its personal burrow, however, annual removal of excess vegetation and soil in artificial burrows increased reuse and occupancy rates in subsequent years in another study of burrowing owls, and suggests that these owls may prefer artificial burrows to natural burrows (Menzel, 2018).

Juvenile frogs in this study had low fidelity to individual artificial burrows. Individual frogs were generally found in different artificial burrows during each survey period. Burrow fidelity has been documented in adult gopher frogs with *R. sevosia* (Richter et al., 2001; Tupy, 2012) and *R. capito* (Humphries & Sisson, 2012). Blihovde (2006) found *R. capito* to use between 1-4 burrows, but suggested disturbance may have interfered with fidelity. The lack of burrow fidelity I observed may be attributed to: 1) the frogs treating artificial burrows differently

than natural burrows; 2) the high density of burrows; 3) disturbance induced stress from removing the frogs from their retreats during recapture events; 4) an artifact of the frogs not migrating from the pond themselves; or 5) differences in behavior between juveniles and adults. Lack of burrow fidelity could suggest that the greater availability of burrows, the better. Augmenting habitats with more burrows could give individuals more choices, which could increase frog densities (and even population size) at those locations.

One objective of my research was to provide management officials and conservation specialists with a new method of improving growth and survivorship rates of *R. sevosia* in fire-suppressed areas, addition of artificial burrows. Placing artificial burrows in uplands of restored wetlands could also make the process of establishing translocated populations more effective by increasing the growth and survival of translocated individuals. While this research provides a critical starting point, identifying artificial burrows as an asset in managing *R. sevosia*, more research is needed to determine the precise depth, density, and distance from breeding ponds to place artificial burrows to fully optimize recovery efforts. The depth of artificial burrows would influence temperature experienced by the occupants. Artificial burrow depth plays a role in occupancy in burrowing owls and temperature is likely driver (Nadeau et al., 2015). Juvenile dusky gopher frogs travel longer distances in fire-suppressed habitat to burrows during migration, likely due to a low burrow density (Roznik & Johnson, 2009b; Tupy, 2012). A high density of artificial burrows placed near ponds in fire-suppressed habitats would likely decrease migration distance and mortality while facilitating growth. Artificial burrow presence can make finding a suitable home much quicker, mitigating the likelihood of predation and desiccation (Rothermel & Luhring, 2005; Roznik & Johnson, 2009a). Introducing these frogs to new or less desirable habitats equipped with artificial burrows could also increase their range. Gopher and

crayfish frogs can use burrows not only as primary homes but also as temporary refuges during migrations (Richter et al., 2001; Heemeyer et al. 2012 Humphries & Sisson, 2012; Tupy, 2012). Placement of artificial burrows along passages from one pond to another could increase the connectivity of habitat. Artificial burrows are likely a beneficial alternative if fire cannot be safely implemented. Artificial burrows would also be valuable in instances where stump removal, bedding, or other forest management practices have reduced the number of burrows (Richter & Jensen, 2005).

This research could be applied to similar species of frog, such as *R. capito*, and to other animals that are dependent on burrows or prescribed fire. Other burrowing animals may benefit from the placement of artificial burrows in these longleaf pine communities. These holes could also provide small fauna with refuge during intense fires. On several surveys, southern toads (*Anaxyrus terrestris*), as well as various arthropod taxa, were found occupying artificial burrows in both habitat types.

Many amphibians are constantly under environmental and anthropogenic stressors, leading to large declines in both population sizes and ranges (Stuart et al., 2004). Understanding the effects habitat has on these animals provides crucial insights to enable improved management plans and practices. I believe that placement of artificial burrows, especially in fire-suppressed areas or less suitable habitats, could work to alleviate some of the stresses dusky gopher frogs endure. Artificial burrows integrated with fire-management was an effective method of increasing survivorship rates in the dusky gopher frog and this model could be replicated to assist in the conservation of species with similar ecological needs. Artificial burrows and fire management were also correlated with increased growth of this critically endangered species. The results of this study provide direct evidence supporting both the use of prescribed fire and

burrow density augmentation in restorative habitat management for recovery of the dusky gopher frog.

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APPENDIX

Monitoring Foraging Excursions Using Camera Traps

I placed a single motion-activated camera in each enclosure, in close proximity to an occupied burrow, to assist in determining the habits and behaviors of this cryptic species. The overall purpose of the cameras was to determine mean times that the frogs spent away from burrows and to compare those times between the fire-maintained and fire-suppressed habitats. I anticipated juvenile frogs would spend less time foraging for food in fire-maintained enclosures because arthropod abundance would be greater. It is also possible that thermal differences affect the frogs' activity pattern. In the summer when it is cooler in the fire-suppressed habitat, frogs may remain outside of their burrows for longer intervals as compensation for thermoregulatory needs. Perhaps in the cooler months, frogs in the fire-suppressed habitat spend more time in their burrows as it would take longer for the ground surface to reach a suitable temperature.

In enclosures without artificial burrows, the camera was placed next to a natural burrow of known occupancy. Each camera was fitted to a steel box, wrapped with a python lock, and camouflaged to mitigate risk of damage or theft. The contents of each camera were collected and analyzed to determine times that focal individuals spent away from their burrows. Cameras were repositioned approximately halfway through the experiment (October 15, 2018) if they had not recorded any frogs. Cameras were deployed from July 8, 2018 – January 3, 2019.

Camera traps did not capture enough significant footage of frogs to make any meaningful comparisons between the two habitats. While the cameras captured several interesting interspecific interactions, they did not capture frogs entering or leaving their burrows as expected. The majority of the data collected by the motion sensor traps were the result of the

cameras being triggered by plant material swaying in the wind. This may have been a result of the high sensitivity settings of the cameras motion sensor. There were only several occasions where cameras captured a frog on film. Trail cameras are typically used to record large game or nuisance species. As a result, cameras were set at a high sensitivity to capture the much smaller, juvenile frogs. Several studies have successfully captured the behavior of adult *Rana areolatus*, a similar species of burrowing frogs, using similar techniques (Hoffman et al., 2010; Engbrecht & Lannoo, 2012). Cameras are much more likely to pick up larger adult individuals than juveniles. It is possible, although unlikely, that poor placement of the cameras could have played a role in the lack of data obtained.

Footage failure may have also been attributed to a combination of unanticipated things; 1) Burrow fidelity was not consistent throughout this study. The frogs may have moved to another burrow in the enclosure sometime after the camera was positioned. 2) The frogs were too small to reliably trigger the motion sensors of the cameras. Perhaps more meaningful footage would be collected with cameras specifically designed for a purpose other than game species or with cameras capturing images at designated intervals.